Variability of egg escapement, fishing mortality and spawning population in the market squid fishery in the California Current Ecosystem

Emmanis Dorval[A,B], *Paul R. Crone*[A] *and Jennifer D. McDaniel*[A]

[A]Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA.
[B]Corresponding author. Email: Emmanis.Dorval@noaa.gov

Abstract. With an average yield of 70 000 Mt from 1999 to 2006, market squid (*Doryteuthis opalescens*) represents one of the most commercially valuable and biologically productive populations off California. An egg escapement model was developed for evaluating the population's reproductive response to varying levels of fishing pressure and, potentially, for aiding management of the fishery. The model is founded on eggs-per-recruit theory, assuming catch fecundity is related to daily-based fishing mortality (F), i.e. analysis generated estimates of proportional egg escapement, $S(F)$, as a function of F per quarter from 1999 to 2006 in three spawning grounds off northern and southern California. Fishing pressure was generally high, with mean derived F ranging from 0.20 to 6 per day. Mean estimated $S(F)$ ranged from 0.08 to 0.75, but in most quarters was higher than 0.30. The classical model was extended for estimating absolute abundance of the resource based on F. Market squid were more abundant in southern California, where mean spawning stock peaked at 1.50×10^9 females, ~108 000 and 130 000 Mt in autumn 2000 and winter 2005 respectively. Although time demanding, this per-recruit analysis represents an effective approach for monitoring reproductive outputs and for aiding stock status determinations of harvested market squid.

Additional keywords: catch fecundity, determinate fecundity, eggs-per-recruit, market squid, proportional egg escapement.

Introduction

Market squid, *Doryteuthis (*formerly, *Loligo) opalescens*, is a short-lived, semelparous species that is distributed along the Pacific coast of North America, from Mexico to Canada (Anderson 2000). Market squid support one of the most important coastal pelagic fisheries in the California Current Ecosystem (Fig. 1). Although the fishery expanded in the early 1960s, scientific sampling occurred in Monterey only inter-mittently from 1948 to 1957, 1973 to 1975, and 1989 to 1994. A design-based sampling program of the catch for estimating fishery and biological parameters has been systematically implemented since the late 1990s, a period of substantial increase in landings and market value for squid around the world (Butler *et al.* 1999; Rodhouse 2001). The fishery targets spawning aggregations directly on egg beds, using both attractor (light) and fishing (purse seine) vessels. Since 1998, the California fishery has been monitored by the California Department of Fish and Game (CDFG), with mandatory log-books and sampling of landings. A series of fishery control rules has been in place since the 1990s, which includes an annual catch limit, as well as specific spatial and temporal fishing constraints. In 2005, a fishery management plan (FMP) was adopted that set the annual catch limit at 107 048 Mt (118 000 short tons), maintained weekend closures, included light and gear restrictions, and limited fishery participation with a restricted access program (CDFG 2005). From 1999 to 2006, annual landings averaged 70 000 Mt, with ex-vessel prices ranging from \$220 to \$640 per Mt. Although effort remained relatively at the same level (i.e. restricted to 55 vessels, 18 brail vessels and 34 light boats; CDFG 2005), in most years, landings were substantially lower than the allowable catch. This is not only because the catch limit was based on a 3-year average catch from 1999 to 2002, but also because the fishery typically stops operating when available biomass exceeds market demand.

Standardised catch-effort data are not reliable proxies for market squid population abundance, given exploitation rates in the fishery are strongly influenced by market demand, proces-sing capacity and availability. When demand is low, fishers usually stop targeting market squid, redirecting their efforts towards other coastal pelagic species (CPS). When landings approach processing capacity, price drops and fishers cease operations for squid, even though abundance and/or availability to the fishery are not limiting factors. At low availability, which is determined by the timing, duration and location of spawning events, the redirection of effort is usually to lower-valued CPS (e.g. Pacific mackerel and Pacific sardine). Hence, typical depletion-based methods that are useful in assessing squid fisheries in other Oceans (Agnew *et al.* 1998b; Young *et al.*
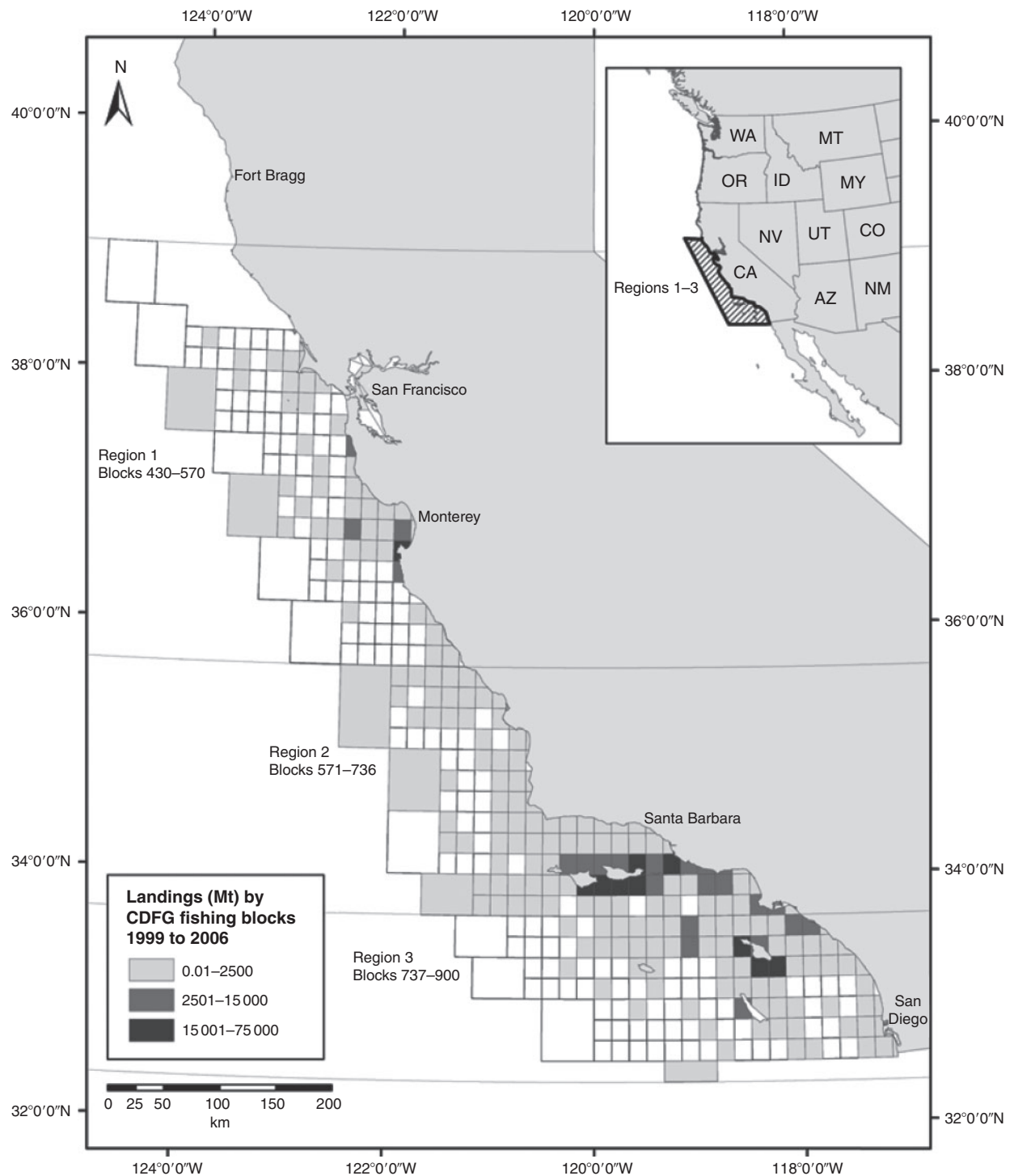
Fig. 1. California fishing block map, showing the location of fishing and the spatial variation of market squid catch (Mt) from 1999 to 2006 in three major spawning grounds (Regions).

2004) are not generally applicable for evaluating the status of the market squid population off California. Finally, other data sources and time series are not generally available for population analysis, which precludes developing highly-parameterised

fishery models, such as multiple data source, fully-integrated, forward-simulation predictive models.

Market squid live on average 6 months (Butler *et al.* 1999; Jackson and Domeier 2003) and predominantly recruit in

spring–summer in northern California (Monterey) and in autumn–winter in southern California, along the Channel Islands (Reiss *et al.* 2004; Foote *et al.* 2006). Following recruitment, mature squid aggregate in shallow coastal waters, where females lay egg cases in clutches for approximately 2–3 days and die after spawning (Jackson 1998; Macewicz *et al.* 2004). There are no overlapping generations in the fishery, and the sustainability of the California market squid population is highly dependent on seasonal recruitments. Market squid fecundity is fixed (determinate) at sexual maturity (Knipe and Beeman 1978; Macewicz *et al.* 2004). The minimum size of oocytes in market squid ovaries increases after the onset of yolking. Primary oogonia are absent in ovaries of mature females, indicating that new oocytes are not produced. Potential fecundity (E_p) is defined as the standing stock of oocytes of all stages in the ovary of mature pre-ovulatory female squid just before the first ovulation and is estimated from histological analysis of the ovaries. Once E_p is known, the proportion of eggs spawned by mature squid before capture (proportional egg escapement, $S(F)$) can be quantified in the fishery (Macewicz *et al.* 2004).

An egg escapement model was developed to evaluate the population dynamics of this species and, potentially, as an in-season management tool for this fishery (Macewicz *et al.* 2004; Maxwell *et al.* 2005). The model was founded on classical per-recruit theory (Beverton and Holt 1957; Sissenwine and Shepherd 1987; Gabriel *et al.* 1989), coupled with the assumption that catch fecundity (θ, the number of oocytes and ova in the ovaries and oviducts of harvested females) is related to daily-based fishing mortality (F) and can be used to develop proxies for F-based biological reference points. The egg escapement model differs from more traditional fishery models because fishing mortality is directly inferred from catch fecundity. The egg escapement model relies on biological information collected from both fishery-dependent and -independent sources to determine fishing mortality (F) and proportional egg escapement ($S(F)$) exhibited by the overall fishery. Given mature squid are likely vulnerable to the fishery for only a few days (Jackson 1998; Macewicz *et al.* 2004), the egg escapement model was developed based on a daily time-step. Therefore, in this study, mortality rates (F, M) and the egg laying rate (v) are accordingly expressed on a daily time scale (see Table 1).

The primary objective of this research was to apply the egg escapement model to the entire California market squid fishery to examine parameter variability, both spatially and temporally. An initial egg escapement model (Macewicz *et al.* 2004; Maxwell *et al.* 2005) was based on a limited dataset that spanned from 1998 to 1999 and included samples from strictly the southern California Bight. Since that time, additional data were collected, allowing the model to be evaluated on a broader spatial–temporal framework.

A secondary objective of this study was to evaluate egg escapement results in the context of biological reference points (BRPs), e.g. fishery operations that result in egg escapement at or above a sustainable threshold. That is, in 2001, management bodies considered a preliminary target of $F_{0.30}$ (F that would allow a proportional egg escapement of 30% in the fishery), which has been informally included in the market squid management as a BRP (CPS-SAFE 2002; CDFG 2005). Finally,

Table 1.   List and description of symbols used in applying the egg escapement model to the market squid fishery off California

Notation	Description
a	Adult
C	Total catch in number
CI	Confidence Interval
f	Females
G	Gonad weight (g)
i	Day in which a cohort becomes mature
j	Juvenile
L	Total landings (Mt)
m	Males
MC	Mantle condition index
ML	Mantle length
q	Quarter
r	Fishing region
t	Day in the fishery
t_{max}	Maximum age in the fishery
t_{min}	Minimum age in the fishery
τ	The upper $\alpha/2$ of the Student's distribution
Variable	
E	Number of eggs spawned
$E(F)$	Eggs-per-recruit at a given F
p	Proportion
ε	Residual fecundity
W	Market squid body weight (g)
N^j	Arbitrary number of juveniles used in model runs
n	Number of sampling units
k	Number of females sub-sampled per sampling unit
Parameter	
E_p	Potential fecundity
F	Instantaneous daily fishing mortality
M	Instantaneous daily natural mortality
$S(F)$	Proportional egg escapement
SSA_f	Spawning stock abundance of females
SSB_f	Spawning stock biomass of females
v	Daily egg laying rate
σ	Standard deviation
θ^{mod}	Mean catch fecundity computed from model runs
θ^{bio}	Mean catch fecundity computed from market squid biological characteristics

because fishing mortality can be directly inferred from catch fecundity in per-recruit analysis, a third objective of this study was to estimate (absolute) population abundance and biomass of the market squid resource off California.

Materials and methods

Model overview

The method described by Maxwell *et al.* (2005) is presented below. Eggs-per-recruit estimates were derived from simulated data that addressed this species' biology, including: (1) fecundity and egg production; (2) growth and maturation; and (3) recruitment dynamics. In the model, market squid were assumed to recruit (to the fishery) at 120 days of age (t_{min}), live of up to 360 days (t_{max} or maximum longevity), and all females reach a maturity threshold and stop growing at 10 cm in mantle

length. Immature squid growth (mantle length) was modelled as a two-parameter exponential curve using Eqn 1.

$$ML_t^j = 3 \times e^{0.019t}, \tag{1}$$

where *ML* is the mantle length of a juvenile squid *j* at day *t*.

The fraction of squid that became mature was computed daily, before natural and fishing mortality took place. The number of juvenile females that recruited to the fishery was set arbitrarily to 1000 (N^j). Abundance of mature squid was calculated in the model in terms of (daily) maturity cohorts, i.e. a group of females that mature on the same day. Because the market squid fishery does not target juveniles, vulnerability of immature and mature squid to the fishery was set to 0 and 1 respectively in all model runs.

Potential fecundity (E_p) was defined as the total number of oocytes of all stages (collectively, number of eggs) in the ovary of a mature, pre-ovulatory female squid. Following Macewicz *et al.* (2004), potential fecundity was assumed to be linearly related to *ML*. In this study, we included 21 additional mature pre-ovulatory females collected during spring research surveys conducted along the coast of Washington and Oregon in 2004 and southern California in 2005, i.e. pre-ovulatory females are difficult to obtain in the field, given once on the spawning grounds, females quickly produce an initial clutch of eggs. Gonads from all samples were stored in formalin before counting the number of eggs in the laboratory. Given the single factor *ML* in the linear regression model did not account for much of the overall variability in the response variable E_p (see Results), we parameterised the egg escapement model using the mean of potential fecundity and associated standard error estimated from actual laboratory counts of eggs.

Additionally, in this analysis, mature females were assumed to lay eggs at a constant daily rate (*v*). The number of eggs in the ovary and oviduct of a female following a spawning event was defined as the residual fecundity. At the beginning of each day, the total number of eggs in the reproductive tracts of all females was estimated in each maturity cohort. Taking into account egg losses to spawning, as well as to natural and fishing mortality, catch fecundity was estimated using Eqn 2.

$$\theta_{i,t}^{mod} = \frac{\varepsilon_{i,t} \times (F + M^a)(1 - e^{-(v + F + M^a)})}{(v + F + M^a)(1 - e^{-(F + M^a)})}, \tag{2}$$

where $\varepsilon_{i,t}$ is the residual fecundity for females that matured on day *i*, and θ^{mod} indicates that catch fecundity was estimated internally from the egg escapement model.

The total number of eggs that were released before squid were captured was normalised to the number of recruits following classical eggs-per-recruit methods (Gabriel *et al.* 1989). Likewise, the number of spawned eggs-per-recruit at a particular fishing mortality rate was calculated as *E(F)* using Eqn 3.

$$E(F) = \frac{\sum_{t=t_{min}}^{t_{max}} \sum_{i=t}^{t_{max}} E_{i,t}}{N_{t_{min}}^j}, \tag{3}$$

where $E_{i,t}$ is the number of eggs actually spawned during day *t* by a maturity cohort *i*.

This computation of spawned eggs-per-recruit is similar to the spawning unit-per-recruit (*SPR*) concept presented in Sissenwine and Shepherd (1987) and in Mace and Sissenwine (1993). Under such a framework, the number of eggs-per-recruit is maximised at $F = 0$, and the proportional egg escapement, *S(F)*, at a fishing mortality greater than zero ($F > 0$) was estimated using Eqn 4.

$$S(F) = \frac{E(F > 0)}{E(F = 0)}, \tag{4}$$

where *E* is the number of spawned eggs-per-recruit.

Finally, for the purpose of this study, all model runs were parameterised to compute θ^{mod} and *S(F)* as a function of *F*, ranging from 0 to 6. Note that in dynamic pool models, such as per-recruit estimators, *F* is not an estimated parameter *per se*, but rather a control variable in each simulation run, whereby the effects of fixed values of *F* are used to estimate catch fecundity and proportional egg escapement. Further, most calculations were based on the best-case scenario values M^a (0.15) and *v* (0.45) recommended in previous reviews (CPS-SAFE 2002). The preferred M^a (0.15) was within the range of plausible values for natural mortality rates, which was assumed to vary from 0.01 to 0.45 in the market squid fishery. The lower bound of natural mortality was based on $M^a = 0.30$ month^{-1} (i.e. 0.01 day^{-1}) estimated for other congeners of market squid (Brodziak 1998; Agnew *et al.* 1998*a*). Based on energy expenditure during spawning and egg deposition rates, Macewicz *et al.* (2004) determined that the maximum total mortality rate (*F + M*) in the fishery should be ~0.45, which, in the absence of fishing, would correspond to the upper bound of the plausible M^a values. Additionally, sensitivity tests were conducted for two other combinations of natural mortality and egg laying rate, ($M^a = 0.01$, *v* = 0.45) and ($M^a = 0.30$, *v* = 0.45). The egg laying rate was kept constant, given all squid in the collected samples had a chance to spawn, i.e. Macewicz *et al.* (2004) determined female squid spawned roughly 36% of their potential fecundity during the first day of egg deposition ($1 - 0.36 = e^{-0.45}$). If not otherwise indicated, all other parameters were set to default values used in Maxwell *et al.* (2005).

Fishery data

Commercial catches of market squid were collected by CDFG from 1999 to 2006. Market squid were sampled in three major ports: Monterey, Santa Barbara, and Los Alamitos. In each area, at least 12 sampling days were scheduled each month. Two boats were randomly selected per day and port area, and 30 individual squid were collected randomly from a vessel (Kong *et al.* 2003). Measurements were taken of each squid from a boat sample, including: mantle length (*ML*) in mm; bodyweight in g; sex determination via visual observations of gonads; and finally, a sub-sample of six squid (one male and five females) was randomly collected for subsequent maturity assessment and catch fecundity estimation.

The three ports are not always a good representation of mutually exclusive fishing areas in the market squid fishery, given vessels from different ports often operate in the same general vicinity. Thus, all squid samples were assigned an

explicit fishing locale based on finer scale spatial (CDFG) blocks. Finally, the collected data were sub-sampled using the following spatial–temporal framework (Fig. 1):

Region 1: south of Bodega Bay to Point Piedras (CDFG blocks 430–570);
Region 2: Santa Barbara, Los Angeles, and the northern Channel Islands (CDFG blocks 571–736); and
Region 3: San Diego and the southern Channel Islands (CDFG blocks 737–900).

Although the egg escapement model provides estimates of fishery parameters based on a daily time scale, it was not practical to sample the fishery every day or to process all samples collected in the field. Therefore, randomly selected samples from the archived collection were analysed by season (i.e. calendar year quarter) within each Region. We defined a sampling unit as a boat trip selected in a given Region. A minimum of 12 sampling units (~60 female squid) per Region/quarter was adequate to estimate mantle condition index and gonad weight with sufficient precision (CV < 25%).

Fishery parameter estimation

Laboratory procedures were conducted at the National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center (SWFSC) in La Jolla, CA. Gonad samples were measured for weight (G) in g. Mantle punches were oven-dried at 56°C for 14 days and weighed dry (g) to provide a mantle condition index (MC). Following Macewicz *et al.* (2004), the catch fecundity of a mature squid was assumed to be a direct function of MC and G. The mean catch fecundity (θ^{bio}) was estimated in Region r and quarter q using Eqn 5.

$$\theta_{r,q}^{bio} = \frac{1}{n}\left(\sum_{u=1}^{n}\left(\frac{1}{5}\sum_{y=1}^{k=5}\left(378.28 \times e^{\left(2.33 \times MC_y + 0.245 \times G_y - 0.24 \times MC_y \times G_y\right)}\right)\right)\right),$$
(5)

where *bio* indicates catch fecundity was computed from biological characteristics of market squid samples, k is the number of females sub-sampled for estimating catch fecundity per sampling unit and n is the number of sampling units per Region and quarter.

A 95% confidence interval (CI) for mean catch fecundity (θ^{bio}) was estimated using Eqn 6.

$$\theta_{r,q}^{bio} \pm \tau \times \frac{\sigma}{\sqrt{n}},$$
(6)

where τ is the upper $\alpha/2$ of the Student's t distribution with $n-1$ degrees of freedom.

The mean catch fecundity estimated from Eqn 5 was matched with its corresponding value in Eqn 2 to determine the mean daily fishing mortality ($F_{r,q}$), and estimate the mean egg escapement $S(F_{r,q})$ that occurred in Region r and quarter q. The 95% CIs of θ^{bio} were used to produce analogous CIs for $F_{r,q}$ and $S(F_{r,q})$. Finally, CIs were not typically calculated for fishery parameters when the number of sampling units was less than 12.

Because squid are semelparous and each maturity cohort was assumed to spawn over a roughly 2-day timeframe and subsequently die (Macewicz *et al.* 2004), the estimate of mean fishing mortality ($F_{r,q}$) was interpreted as the average daily fishing mortality that any maturity cohort would have experienced cumulatively over its lifetime in the fishery in a given Region and quarter. A similar assumption was also made for natural mortality.

Mean proportion and mean weight of market squid were estimated for both sexes. These estimates were then applied to landing data to compute the number of females in the catch ($C_{f,r,q}$) per Region and quarter using Eqn 7.

$$C_{f,r,q} = \frac{L_{r,q}}{\bar{p}_{f,q} \times \bar{w}_{f,q} + \bar{p}_{m,q} \times \bar{w}_{m,q}} \times \bar{p}_{f,q},$$
(7)

where f and m indicates females and males respectively, L is the total landings in Mt, w is bodyweight and p the proportion of males or females in the landings.

Based on Baranov's catch equation (Quinn and Deriso 1999), the spawning stock abundance (SSA_f in numbers) was computed (1999–06) using Eqn 8.

$$SSA_{f,r,q} = \frac{(M_{r,q}^a + F_{r,q}) \times C_{f,r,q}}{F_{r,q} \times \left(1 - e^{(M_{r,q}^a - F_{r,q})}\right)},$$
(8)

where parameters are as defined previously. Finally, Eqn 8 was used to estimate female spawning stock biomass (SSB_f) by expressing catch in weight instead of number.

Results

Composition of the catch

The market squid fishery typically targets mature individuals, as was the case for landings from 1999–2006 used in this study, with catches being highly variable, both temporally and spatially (Fig. 2). Immature squid accounted for less than 5% of the catch in most quarters. The mean proportion of females in the catch ranged from 20 to 55% in Region 1, 36 to 52% in Region 2 and 25 to 57% in Region 3. Females were generally smaller in size than males. Quarterly estimates of mean bodyweight of females from 2000 to 2006 ranged from 25 to 45 g in Region 1, 26 to 52 g in Region 2 and 26 to 58 g in Region 3. Quarterly estimates of mean bodyweight of females were significantly different among years ($P = 0.001$), but not significantly different between Regions ($P = 0.630$).

Potential fecundity estimates

The slope of the linear regression of E_p on ML was significantly different ($P = 0.015$) from 0. However, the linear model did not account for a substantial amount of the total variation in the response variable E_p, i.e. $R^2 = 17\%$ (Fig. 3a). Further, assuming a zero intercept did not significantly improve the level of variability explained by this linear relationship. Results indicated that small market squid may have a similar level of E_p as large individuals, and that fecundity is variable temporally and spatially as shown in the southern California samples (Fig. 3b). Mean E_p and standard error were 3705 and 165 respectively.
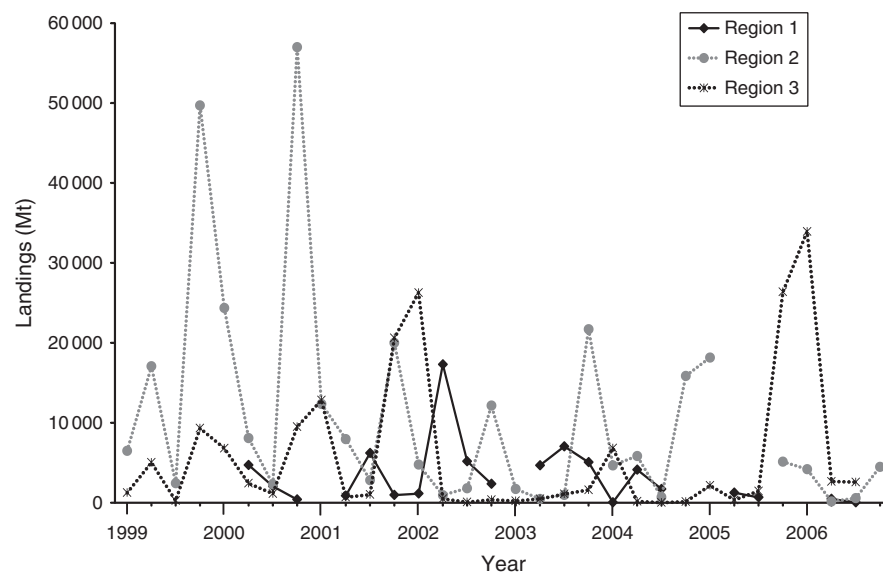
Fig. 2. Landings (Mt) of market squid in California by Region and quarter from 1999 to 2006. The first quarter of the year is marked with a major tick, followed by minor ticks indicating the next three quarters of the respective year.
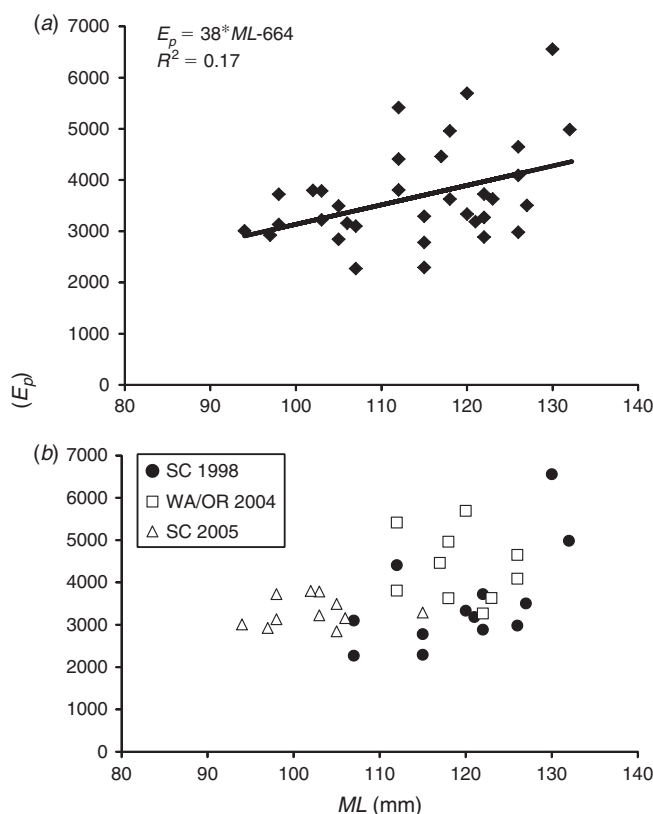

Fig. 3. Relationship between potential fecundity (E_p) and dorsal mantle length (ML, panel *a*). Potential fecundity was estimated from direct counts of oocytes in pre-ovulatory mature females collected in three areas off the USA Pacific coast (panel *b*): southern California (SC); and Washington/Oregon (WA/OR).

Model parameter estimates

The egg escapement model was parameterised using the mean potential fecundity and standard error, i.e. 3705 ± 165 eggs. As expected, mean catch fecundity (θ^{mod}) increased and proportional egg escapement, $S(F)$, decreased with increasing F (Fig. 4*a*, *b*). When F was kept constant, both mean catch fecundity and $S(F)$ increased as M^a increased (Fig. 4*a*, *b*). For θ^{mod}, differences in trends generated from the model scenarios (i.e. M^a and v) were observed up to relatively low levels of fishing pressure, followed by similar asymptotes at roughly $F = 1$ (Fig. 4*a*). Conversely, for $S(F)$, trends between the model scenarios were most different within a middle range of F (roughly, $F = 0.5$–3) and similar trajectories at the lower and higher boundaries of F (Fig. 4*b*).

Fishery parameter estimates

Based on the best case scenario ($M^a = 0.15$ and $v = 0.45$), there was more variability in F within than between Regions. In most quarters, mean estimates of F were high and generally similar across Regions, ranging from a minimum of 0.20 to a maximum of 6 (Fig. 5*a*–*c*).

Similar to fishing mortality, $S(F)$ was more variable within than between Regions. Mean estimates of $S(F)$ were on average higher than 0.30, ranging from 0.08 to 0.64 in Region 1, 0.09 to 0.75 in Region 2 and 0 to 0.75 in Region 3. All three Regions showed a slight upward trend in egg escapement from 2000 to 2006 (Fig. 6*a*–*c*).

Estimates of abundance and biomass based on the best case scenario ($M^a = 0.15$, $v = 0.45$) were generally different among Regions, with most squid occurring in Regions 2 and 3 (Fig. 7*a*–*c*). Highest peaks of abundance were observed in spring 2002 in Region 1, autumn 2000 and winter 2005 in Region 2, and winter 2002 and winter 2006 in Region 3. Abundance usually
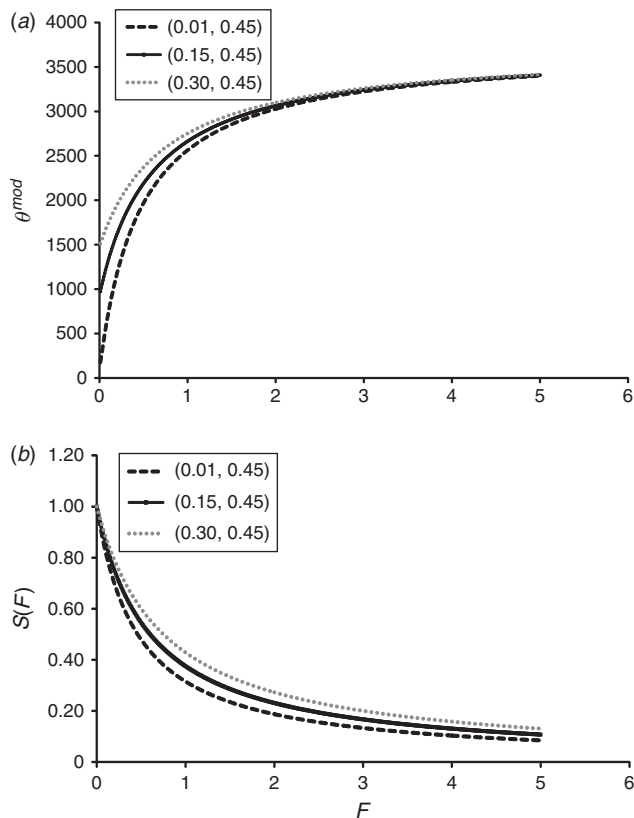
Fig. 4. Trajectories of catch fecundity (θ^{mod}, panel *a*) and proportional egg escapement ($S(F)$, panel *b*) as functions of fishing mortality (F) for three different combinations of natural mortality and egg laying rate (M^a, v): (0.01, 0.45), (0.15, 0.45), and (0.30, 0.45).

peaked in Region 3, one quarter later than in Region 2, indicating a southward trend in spawning by the market squid population within each calendar year.

Relatively low estimates of spawning biomass were similar across the three Regions (34–116 Mt), with relatively high estimates being markedly different (e.g. maximum estimated SSB_f was 19 528, 127 394, and 70 550 Mt in Regions 1, 2 and 3 respectively). Finally, SSB_f increased as M increased (Table 2).

Discussion

Potential fecundity

Assuming a strictly linear relationship between potential fecundity (E_p) and mantle length (ML) of market squid may be misleading, given the substantial amount of unexplained variation in the regression model ($R^2 = 17\%$). These results indicate E_p is highly variable annually and further, that E_p may not be size specific, i.e. small squid may have similar fecundity thresholds as large squid. Thus, it may not be appropriate to predict fecundity from mantle length alone, particularly when using samples that were collected across a protracted timeframe.

Studies that have addressed the relationship of fecundity and ML in loliginids have resulted in mixed findings, even when conducted on the same species. For example, Coelho *et al.* (1994) found a strong positive correlation ($r = 0.87$) between
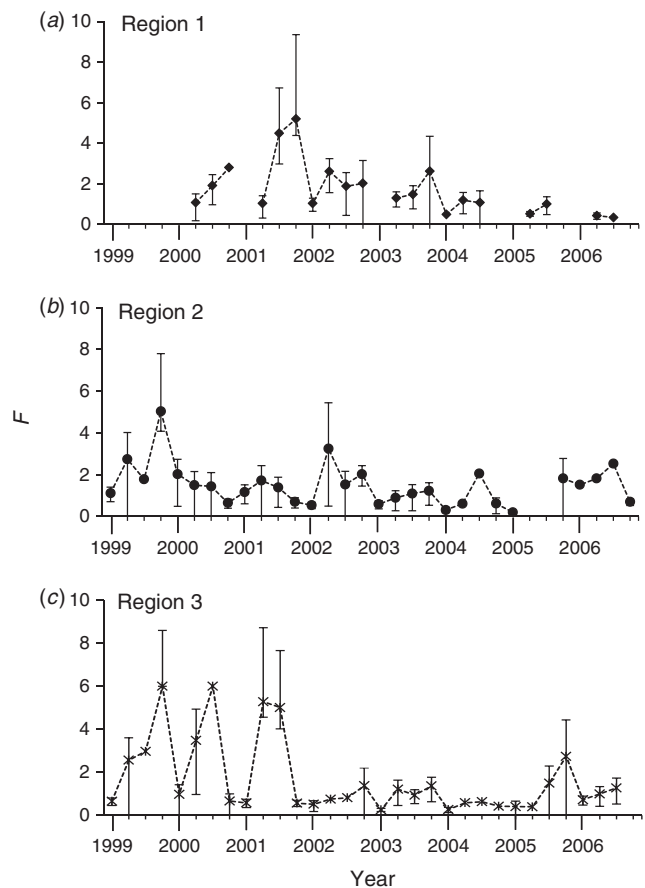

Fig. 5. Levels of fishing (daily) mortality, *F*, for Regions/quarters (panels *a–c*) from the egg escapement model, and generated from the best case scenario ($M^a = 0.15$, $v = 0.45$). The first quarter of the year is marked with a major tick, followed by minor ticks indicating the next three quarters of the respective year.

fecundity and ML of *Loligo vulgaris* collected in southern Portugal in 1991–92, whereas Šifner and Vrgoč (2004) detected a weak positive correlation ($r = 0.19$) between these two parameters in *L. vulgaris* sampled in the Adriatic Sea in 1998–2000. Potential fecundity of squid is poorly understood at this time and is likely influenced by other critical factors and interactions associated with both squid biology and oceanographic conditions. Mature pre-ovulatory squid used in this study were collected from 1998 to 2005 and across a wide range of environmental conditions from California to Washington. However, limited samples of pre-ovulatory females available for this study ($n = 34$) precluded adequately investigating the effects of the physical environment on potential fecundity.

Finally, a major analytical shortcoming of the linear relationship of E_p and ML (Fig. 4) was that in many cases, the regression model predicted values that were lower than the observed catch fecundity. When such bias occurred, matching catch fecundity between model and laboratory efforts necessarily resulted in unrealistic estimates of fishing mortality and proportional egg escapement. Therefore, we considered direct counts of oocytes in the laboratory as the best method currently for estimating market squid potential fecundity in the fishery.
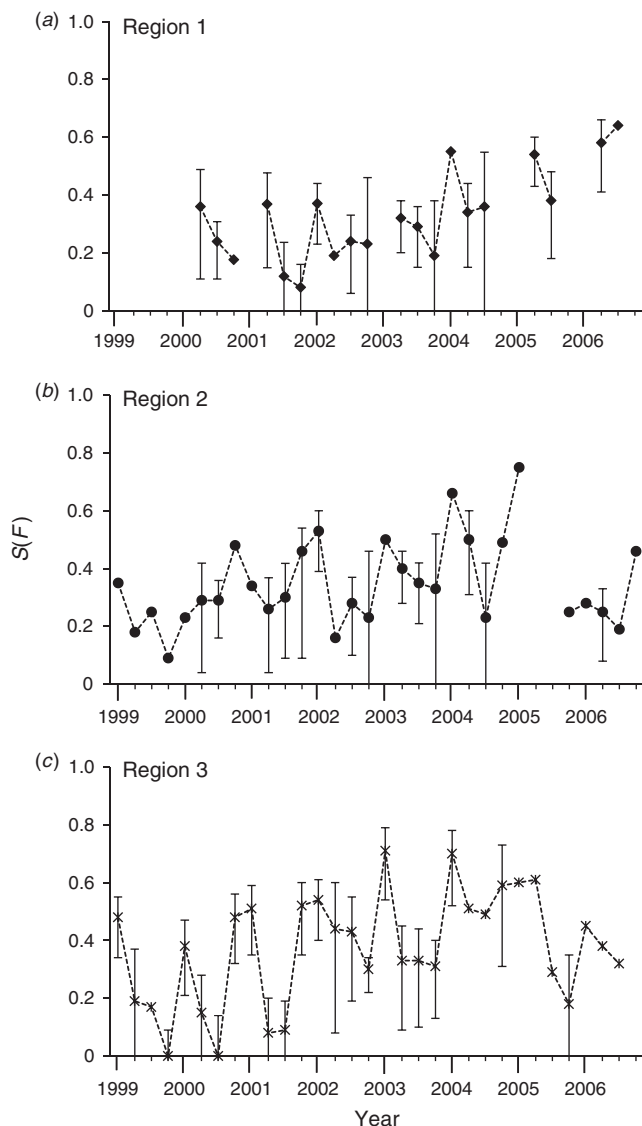
Fig. 6. Estimates of mean proportional egg escapement, $S(F)$, for Regions/quarters (panels *a–c*) from the egg escapement model, and generated from the best case scenario ($M^a = 0.15$, $v = 0.45$). The first quarter of the year is marked with a major tick, followed by minor ticks indicating the next three quarters of the respective year.

Fig. 7. Estimates of mean number of female spawners for Regions/quarters (panels *a–c*) from the egg escapement model, and generated from the best case scenario ($M^a = 0.15$, $v = 0.45$). The first quarter of the year is marked with a major tick, followed by minor ticks indicating the next three quarters of the respective year.

Model parameters

Although the linear relationship between potential fecundity and mantle length was not relied upon in this study, estimates of proportional egg escapement at a given level of daily fishing mortality were generally similar to previous research (Maxwell *et al.* 2005). As expected, increasing fishing mortality (*F*) resulted in increasing catch fecundity (θ^{mod}) and decreasing proportional egg escapement, $S(F)$. In cases when *F* was kept constant, an increase in natural mortality (*M*) resulted in an increase in catch fecundity and proportional egg escapement. These trends can be partly attributed to relatively smaller decreases in proportion of spawned eggs-per-recruit relative to the maximum attainable as *M* increases (e.g. Maxwell *et al.*
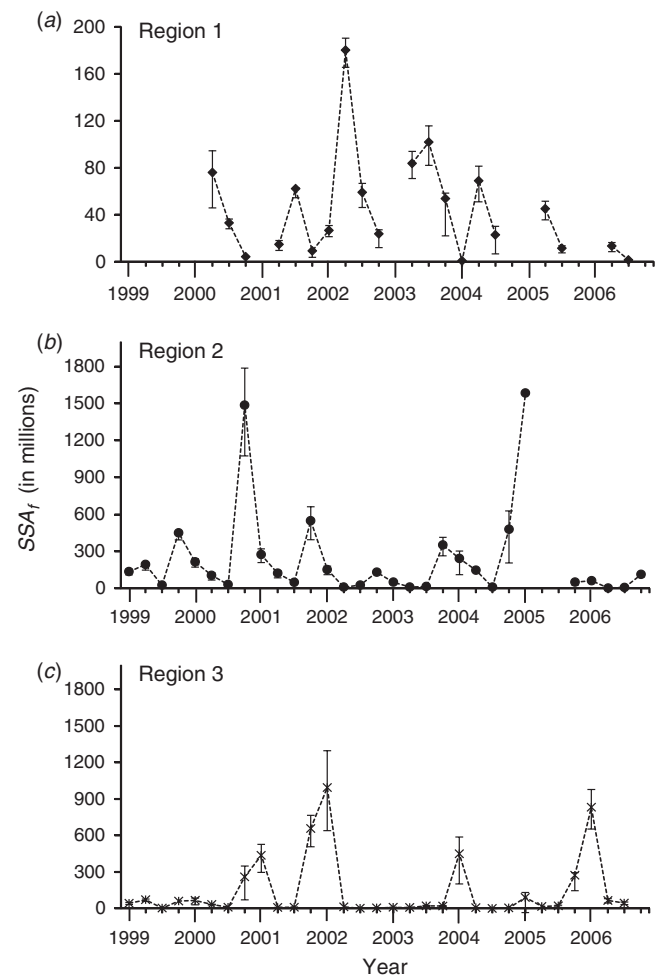
2005), i.e. the population's reproductive response to increased intrinsic mortality, within noted ranges of *F*, is increased proportional egg escapement in the population and yield to the fishery. Higher mortality compensated by higher productivity has been previously demonstrated in semelparous squid (e.g. Murphy and Rodhouse 1999), and has been commonly observed in arthropod populations (e.g. Frago *et al.* 2011). However, the mechanisms that may control this phenomenon in the market squid population are not well understood and thus warrant further investigations.

Fishery parameters

Market squid spawners experienced high levels of fishing mortality (*F*) in most quarters across all Regions, with *F* being more variable within than between Regions. These spatial variations in *F* reflect the dynamics of the overall California fishery to date. Fishers typically search for and concentrate their effort in areas where mature squid aggregate in high densities. These fishing operations resulted in a temporal fishery, with most

Table 2. Spawning stock biomass (SSB_f, Mt) estimated for three levels of natural mortality, *M* (0.01, 0.15, 0.30), and a constant egg laying rate (*v*) of 0.45

n indicates the number of sampling units

Year	Quarter	Region 1 SSB_f				Region 2 SSB_f				Region 3 SSB_f			
		n	0.01	0.15	0.30	*n*	0.01	0.15	0.30	*n*	0.01	0.15	0.30
1999	1					32	9143	10 245	11 829	48	2299	2794	3633
1999	2					26	18 143	19 070	20 175	39	5407	5703	6058
1999	3					9	2868	3094	3378	3	263	276	291
1999	4					29	49 966	51 476	52 594	11	9341	9566	9796
2000	1					30	27 598	29 501	31 855	23	10 193	11 664	13 798
2000	2	18	6743	7626	8869	30	10 069	11 009	12 233	18	2493	2593	2710
2000	3	14	2365	2538	2822	15	2900	3182	3552	10	1133	1161	1189
2000	4	2	419	440	465	57	104 817	127 394	194 164	13	17 317	20 991	27 165
2001	1					32	16 996	19 030	21 829	30	25 608	31 588	43 722
2001	2	14	1274	1447	1694	32	9464	10 234	11 244	12	685	705	718
2001	3	36	6277	6473	6696	26	3623	3988	4470	18	1022	1053	1079
2001	4	12	960	988	1008	41	35 375	42 450	104 094	30	41 095	51 369	70 162
2002	1	19	1655	1880	2472	35	8312	12 239	16 946	31	55 215	70 372	99 694
2002	2	79	18 533	19 528	20 718	16	987	1030	1079	5	809	960	1199
2002	3	41	5994	6440	6998	21	2252	2458	2725	6	115	135	165
2002	4	12	2679	2864	3094	70	13 777	14 727	16 033	13	474	523	587
2003	1					33	3329	4119	5523	18	683	1066	2664
2003	2	26	6150	6812	7701	12	742	858	1032	22	651	726	824
2003	3	29	8811	9644	10 732	13	1376	1551	1796	26	1654	1903	2269
2003	4	13	5424	5714	6061	35	29 207	32 532	37 050	35	2069	2282	2565
2004	1	1	90	116	167	19	12 950	18 798	36 422	28	20 799	31 999	69 654
2004	2	12	5646	6310	7220	9	11 131	13 686	18 148	6	322	400	550
2004	3	12	2444	2764	3214	1	791	845	911	1	29	35	47
2004	4					12	29 930	36 688	48 397	5	284	379	589
2005	1					7	63 337	107 673	430 691	12	5177	6988	11 181
2005	2	12	2617	3322	4668					9	821	1116	1813
2005	3	12	989	1128	1327					12	1821	1992	2215
2005	4					12	5995	6456	7036	12	28 022	29 453	31 159
2006	1					7	5204	5683	6306	42	59 065	70 550	87 955
2006	2	21	1088	1443	2216	1	189	203	222	17	3935	4491	5294
2006	3	4	116	164	294	3	621	656	697	19	3418	3795	4282
2006	4					14	7936	9523	12 120				

effort occurring in Region 1 during spring and summer, and in Regions 2 and 3 during autumn and winter.

Several factors may explain how the population could sustain such high rates of fishing pressure over the last decade or two without functionally collapsing or reducing reproductive output to some degree. First, the fishery captured mostly adult squid that represented more than 95% of the landings in most quarters and across all Regions, i.e. fishers do not target juvenile squid because they typically have less market value than mature, larger squid. Furthermore, most mature squid that become available to the fishery were able to release a significant proportion of their eggs before being captured (Macewicz *et al.* 2004), which is consistent with the assumption of an egg laying rate of 0.45. Second, since 1998, a 2-day weekend closure has been imposed by CDFG, coupled with the closure of the Channel Islands to fishing activity within 1 mile during the seabird breeding season (CDFG 2005). These management measures are intended to ensure that a substantial amount of eggs escape from fishery harvest and offset some of the negative effects of fishing on the spawning stock and subsequent

recruitment. Third, the origin of market squid that seasonally recruit in the fishery is not well known. Zeidberg and Hammer (2002) found that market squid paralarvae were more abundant close to shore, indicating that they might have been hatched from nearby spawning grounds. However, potential large-scale mixing between the adult populations is not well understood at this time (Warner *et al.* 2009). Finally, the possible biological and physical processes that influence market squid dynamics in the fishery need further research attention to identify and better understand critical mechanisms controlling population size in any given year.

Although variable within Region, proportional egg escapement was generally higher than 0.30 in most quarters, which was above egg escapement (target) levels recommended informally by management (CPS-SAFE 2002; CDFG 2005). Intra-annual variability of recruitment was high for some time periods (quarters/years), but reproductive success was generally observed to increase across quarters in a Region (Fig. 6a–c). Further, results from this study indicated that some critical reproductive outputs (e.g. *S*(*F*)) were similar among fishing

Regions and, thus, spatial dynamics in the overall fishery do not appear to noticeably influence reproductive processes of the overall market squid population. Finally, given the above findings, regional management should not be discounted, rather considered in the context of a single population (Reichow and Smith 2001) that reproduces disproportionately across an extensive spatial range.

The abundance of market squid was derived from fishing mortality inferred from catch fecundity, combined with both biological and landing data. The model generated maximum abundance estimates in southern California in Region 2 during the autumn of 2000 and winter of 2005, when the spawning stock averaged 1.5×10^9 individual females. This abundance level is within a plausible range for short-lived and semelparous squid species. For example, based on classical removal–depletion methods, Agnew *et al.* (1998*a*, 2005) predicted average recruitments as high as 7×10^9 for *L. gahi* in each of two fishing seasons, from 1987 to 1996. Thus, the fishing mortality rates estimated from the egg escapement model ($M^a = 0.15$ and $v = 0.45$ scenario) presented here appear reasonable ones based on previous studies.

Biomass estimation was sensitive to the assumed natural mortality (M^a) rate. Spawning stock biomass (SSB_f) increased as M^a increased, which is necessarily related to the cases for catch fecundity and proportional egg escapement discussed above. Finally, these results further support the closed-area strategy adopted in the current management of market squid (CDFG 2005), i.e. closure of spawning grounds to fishing may result in increased predation mortality (say increasing M^a), ultimately producing a more productive population.

At maximum peaks of abundance, the total spawning stock, including both female and male market squid, may range between 215 000 and 254 000 Mt in a single quarter in the southern Regions (2 and 3). In some quarters, stock biomass in Region 1 was one to two orders of magnitude lower than that of Regions 2 or 3. The current state-imposed catch limit of 107 048 Mt represents an annual quota for the entire California fishery (CDFG 2005). Finally, as communicated above, although some explicit reproductive processes measured on a per-recruit basis were similar across Regions, substantial differences in abundance/biomass between Regions suggests a management scheme based on a single quota applied disproportionately across Regions and noting temporal differences that address this population's life history strategy.

Application of the model

The egg escapement model was originally developed as an in-season management tool, although it has not been used explicitly in developing formal management measures to date. Further the application of the model as a real-time management tool would be costly and time-consuming, primarily due to the type of samples required in the field and subsequent processing in the laboratory. There is a limited time between the initial onset of maturity and actual spawning events, which is inherently problematic for collection of mature, pre-ovulatory females (i.e. this biological attribute may be strongly influenced by prevailing oceanographic conditions and vary over short timeframes). Thus, sampling for pre-ovulatory market squid from independent surveys has a high ratio of cost to collected samples.

It takes a minimum of 14 days to process and estimate the mantle condition index from a sample of market squid. Collection and laboratory analysis of gonad samples usually span over several months. Limited resources, coupled with semelparity of mature squid in the fishery and the abbreviated fishing seasons (3–4 months per Region), has prevented the collection and processing of market squid samples in a timely/practical manner for implementing real time, in-season management. Finally, it is important to note that implementing management adaptively within a year based on biological attributes measured in the landings is necessarily problematic, given this species' very high intrinsic rates of increase and decrease ('boom and bust') based on current environmental conditions.

To some degree, the spatial and temporal scales at which to apply management in the market squid fishery should consider Region-specific approaches, given squid biology, particularly regional differences in estimates of absolute population abundance during the study timeframe. Decadal-based results generated from this study are likely generally applicable over longer time periods; however, further evaluation of reproductive data collected recently and in the near future (e.g. 2010–2015) will be necessary to better assess the plasticity of the estimates generated here. Further, application of the egg escapement model for management purposes should consider the inter-annual variability of proportional egg escapement, because implementing a strict threshold value (e.g. 30%) across long timeframes will likely lead to a less efficient fishery than using more adaptive, time-varying target levels. In this context, the spatial/temporal descriptive statistics generated from this per-recruit study provide underlying datasets for further simulation modelling (e.g. spawner–recruit evaluations) that will be necessary to more objectively determine egg escapement levels that ensure long-term sustainability of the exploited resource. Finally, this analysis provides a straightforward analytical approach for computing estimates of absolute abundance of the spawning population using relatively limited information, i.e. catch and biological time series, and fishing mortality estimates inferred from the eggs-per-recruit methods documented here.

References

Agnew, D. J., Baranowski, R., Beddington, J. R., des Clers, S., and Nolan, C. P. (1998*a*). Approaches to assessing stocks of *Loligo gahi* around the Falkland Islands. *Fisheries Research* **35**, 155–169. doi:10.1016/S0165-7836(98)00083-6

Agnew, D. J., Nolan, C. P., and des Clers, S. (1998*b*). On the problem of identifying and assessing populations of Falkland Island squid *Loligo gahi*. *South African Journal of Marine Science* **20**, 59–66. doi:10.2989/025776198784126412

Agnew, D. J., Hill, S. L., Beddington, J. R., Purchase, L. V., and Wakeford, R. C. (2005). Sustainability and management of southwest Atlantic squid fisheries. *Bulletin of Marine Science* **76**, 579–593.

Anderson, F. E. (2000). Phylogenetic relationships among loliginids (Cephalopoda: Myopsida) based on analyses of multiple data sets. *Zoological Journal of the Linnean Society* **130**, 603–633. doi:10.1111/J.1096-3642.2000.TB02203.X

Beverton, R. J. H., and Holt, S. J. (1957). 'On the Dynamics of Exploited Fish Populations.' (Chapman & Hall: London. Facsimile reprint, 1993.)

Brodziak, J. (1998). Revised biology and management of long-finned squid (*Loligo pealeii*) in the northwest Atlantic. *California Cooperative Oceanic Fisheries Investigations Reports* **39**, 61–70.

Butler, J., Fuller, D., and Yaremko, M. (1999). Age and growth of market squid (*Loligo opalescens*) off California during 1998. *California Cooperative Oceanic Fisheries Investigations Reports* **40**, 191–195.

CDFG (2005). Final draft market squid fishery management plan. State of California – The Resources Agency. Department of Fish and Game, Marine Region, Los Alamitos, CA.

Coelho, M. L., Quintela, J., Bettencourt, V., Olavo, G., and Villa, H. (1994). Population structure, maturation patterns and fecundity of the squid *Loligo vulgaris* from southern Portugal. *Fisheries Research* **21**, 87–102. doi:10.1016/0165-7836(94)90097-3

CPS-SAFE (2002). Status of the Pacific coastal pelagic species fishery and recommended acceptable biological catches. Stock assessment and fishery evaluation 2002. Pacific Fishery Management Council, Portland, OR.

Foote, G. K., Halon, R. T., Iampietro, P. J., and Kvitek, R. G. (2006). Acoustic detection and qualification of benthic egg beds of the squid *Loligo opalescens* in Monterey Bay, California. *The Journal of the Acoustical Society of America* **119**, 844–856. doi:10.1121/1.2149840

Frago, E., Pujade-Villar, J., Guara, M., and Selfa, J. (2011). Providing insights into browntail moth local outbreaks by combining life table data and semi-parametric statistics. *Ecological Entomology* **36**, 188–199. doi:10.1111/J.1365-2311.2010.01259.X

Gabriel, W. L., Sissenwine, M. P., and Overholtz, W. J. (1989). Analysis of spawning biomass per recruit: an example for Georges Bank haddock. *North American Journal of Fisheries Management* **9**, 383–391. doi:10.1577/1548-8675(1989)009<0383:AOSSBP>2.3.CO;2

Jackson, G. D. (1998). Research into the life history of *Loligo opalescens*: where to from here? *California Cooperative Oceanic Fisheries Investigations Reports* **39**, 101–107.

Jackson, G. D., and Domeier, M. L. (2003). The effects of an extraordinary El Niño/La Niña event on the size and growth of the squid *Loligo opalescens* off southern California. *Marine Biology* **142**, 925–935.

Knipe, J. H., and Beeman, R. D. (1978). Histological observations on oogenesis in *Loligo opalescens*. In 'Biological, Oceanographic and Acoustic Aspects of the Market Squid, *Loligo opalescens* Berry'. (Eds C. W. Ricksiek and H. W. Frey.) pp. 23–33. (Fish Bulletin 169. California Department of Fish and Game; Long Beach, CA.)

Kong, C., Bishop, T. L., Larson, M. L., Krauss, J., and Taylor, V. (2003). A guide to port sampling, laboratory sampling procedures, and databases for the market squid fishery. State of California – The Resources Agency. Department of Fish and Game, Marine Region, Los Alamitos, CA.

Mace, P., and Sissenwine, M. P. (1993). How much spawning per recruit is enough? In 'Risk Evaluation and Biological Reference Points'. (Eds S. J. Smith, J. J. Hunt and D. Rivard.) pp. 101–125. (Canadian Special Publication of Fisheries and Aquatic Sciences. 120.)

Macewicz, B. J., Hunter, J. R., Lo, N. C. H., and LaCasella, E. L. (2004). Fecundity, egg deposition, and mortality of market squid (*Loligo opalescens*). *Fishery Bulletin* **102**, 306–327.

Maxwell, M. R., Jacobson, L. D., and Conser, R. (2005). Eggs-per-recruit for management of the California market squid (*Loligo opalescens*). *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1640–1650. doi:10.1139/F05-037

Murphy, E. J., and Rodhouse, P. G. (1999). Rapid selection effects in a short-lived semelparous squid species exposed to exploitation: inferences from the optimization of life-history functions. *Evolutionary Ecology* **13**, 517–537. doi:10.1023/A:1006783902331

Quinn, T. J., and Deriso, R. B. (1999). 'Quantitative Fish Dynamics.' (Oxford University Press; New York.)

Reichow, D., and Smith, M. J. (2001). Microsatellites reveal high levels of gene flow among populations of the California squid, *Loligo opalescens*. *Molecular Ecology* **10**, 1101–1109. doi:10.1046/J.1365-294X.2001.01257.X

Reiss, C. S., Maxwell, M. R., and Hunter, J. H. (2004). Investigating environmental effects on population dynamics of *Loligo opalescens* in the Southern California Bight. *California Cooperative Oceanic Fisheries Investigations Reports* **45**, 87–97.

Rodhouse, P. G. (2001). Managing and forecasting squid fisheries in variable environments. *Fisheries Research* **54**, 3–8. doi:10.1016/S0165-7836(01)00370-8

Šifner, S. K., and Vrgoč, N. (2004). Population structure, maturation and reproduction of the European squid, *Loligo vulgaris*, in the Central Adriatic Sea. *Fisheries Research* **69**, 239–249. doi:10.1016/J.FISHRES.2004.04.011

Sissenwine, M. P., and Shepherd, J. G. (1987). An alternative perspective on recruitment overfishing and biological reference points. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 913–918. doi:10.1139/F87-110

Warner, R. R., Hamilton, S. L., Sheehy, M. S., Zeidberg, L. D., Brady, B. C., and Caselle, J. E. (2009). Geographic variation in natal and early larval trace-elemental signature in the statoliths of the market squid *Dorytheuthis* (formerly *Loligo*) *opalescens*. *Marine Ecology Progress Series* **379**, 109–121. doi:10.3354/MEPS07903

Young, I. A. G., Pierce, G. J., Daly, H. I., Santos, M. B., Key, L. N., Bailey, N., Robin, J. P., Bishop, A. J., Stowasser, J., Nyegaard, N., Cho, S. K., Raseo, M., and Pereira, J. M. F. (2004). Application of depletion method to estimate stock size in the *Loligo forbesi* in Scottish waters (U.K.). *Fisheries Research* **69**, 211–227. doi:10.1016/J.FISHRES.2004.04.013

Zeidberg, L. D., and Hammer, W. M. (2002). Distribution of squid paralarvae, *Loligo opalescens* (Cephalopoda: Myopsida), in the Southern California Bight in the three years following the 1997 El Nino. *Marine Biology* **141**, 111–122.